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EMPHASIZING NEW IDEAS TO STIMULATE RESEARCH IN ECOLOGY

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Understanding ecosystem retrogression

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Abstract. Over time scales of thousands to millions of years, and in the absence of rejuvenating disturbances that initiate primary or early secondary succession, ecosystem properties such as net primary productivity, decomposition, and rates of nutrient cycling undergo substantial declines termed ecosystem retrogression. Retrogression results from the depletion or reduction in the availability of nutrients, and can only be reversed through rejuvenating disturbance that resets the system; this differs from age-related declines in forest productivity that are driven by shorter-term depression of nutrient availability and plant ecophysiological process rates that occur during succession. Here we review and synthesize the findings from studies of long-term chronosequences that include retrogressive stages for systems spanning the boreal, temperate, and subtropical zones. Ecosystem retrogression has been described by ecologists, biogeochemists, geologists, and pedologists, each of which has developed somewhat independent conceptual frameworks; our review seeks to unify this literature in order to better understand the causes and consequences of retrogression. Studies of retrogression have improved our knowledge of how long-term pedogenic changes drive shorter-term biological processes, as well as the consequences of these changes for ecosystem development. Our synthesis also reveals that similar patterns of retrogression (involving reduced soil fertility, predictable shifts in organismic traits, and ecological processes) occur in systems with vastly different climatic regimes, geologic substrates, and vegetation types, even though the timescales and mechanisms driving retrogression may vary greatly among sites. Studies on retrogression also provide evidence that in many regions, high biomass or "climax" forests are often transient, and do not persist indefinitely in the absence of rejuvenating disturbance. Finally, our review highlights that studies on retrogressive chronosequences in contrasting regions provide unparalleled opportunities for developing general principles about the long-term feedbacks between biological communities and pedogenic processes, and how these control ecosystem development.

Key words: carbon; diversity; ecosystem development; nitrogen; nutrient cycling; pedogenesis; phosphorus; plant-soil feedbacks; soil processes; retrogression; stoichiometry; succession.

Introduction

Major disturbances in ecosystems usually induce primary or secondary succession that involves an initial period (often decades to centuries) of progressive

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ecosystem development and then a maximal biomass phase (Walker and del Moral 2003, 2008). Classic views on succession and ecosystem development focused on this "progressive" phase, during which ecosystem biomass increases over time (Warming 1895, Cowles 1899, Clements 1928, Whittaker et al. 1989). More recently, concepts regarding succession have recognized the dynamic nature of plant communities and the importance of local disturbance (Pickett and White 1985, Walker and del Moral 2003), but have still retained a primary focus on the progressive build-up and maximal biomass phases of succession, and accompanying changes in the physicochemical composition of the soils. There are instances where more complex secondary successions are possible or for which disturbance does not necessarily drive secondary succession (e.g., for fire-driven ecosystems in parts of Australia and South Africa: Bond et al. 2005, Whelan and Main 2006). As such, there is a substantial body of literature on the developmental period of succession which is generally characterized by predictable shifts in community composition, biodiversity, and ecosystem processes such as primary productivity, biomass accumulation, nutrient cycling, and decomposition (Walker and Chapin 1987, Wardle 2002, Chapin et al. 2003). These comparatively short-term changes have formed the basis of many concepts in community and ecosystem ecology (e.g., successional processes, ecosystem development, community responses to disturbances), but have also been widely applied in ecosystem management and restoration (e.g., Ehrenfeld and Toth 1997, Suding et al. 2004, Walker et al. 2007, Seastedt et al. 2008, Hobbs et al. 2009).

A growing number of studies indicate that over much longer time scales (i.e., thousands to millions of years), and in the absence of rejuvenating disturbances (i.e., those that are sufficiently severe to induce primary or early secondary succession), ecosystem properties such as net primary productivity (NPP), decomposition and nutrient cycling do not remain constant. Rather, after the maximal biomass phase is reached, ecosystem biomass can undergo a period of substantial decline or "ecosystem retrogression" (Vitousek and Farrington 1997, Wardle et al. 2004; Fig. 1); this decline in biomass over lengthy time scales is what distinguishes retrogressive ecosystems from those in which biomass is inherently low due to other factors (e.g., climate). This retrogression is also quite distinct from age-related declines in forest biomass or productivity that frequently occur over far shorter time scales as a result of changes in the physiological properties of plants (e.g., declining photosynthesis to respiration ratios, increasing stomatal limitation as trees age), increasing hydraulic limitation as trees grow taller, and reductions in soil nutrient mineralization rates (e.g., Brais et al. 1995, Gower et al. 1996, Ryan et al. 1997, 2004, Magnani et al. 2000). In contrast to these age-related declines, ecosystem retrogression involves multiple generations of the dominant plant species and is largely a pedogenically driven process.

Ecosystem retrogression has been studied mostly in well characterized chronosequences, or sequences of soils of different ages since formation. Such studies focused on long-term chronosequences serve as "space for time" substitutions (Pickett 1989, Fukami and Wardle 2005) that yield significant insights into pedogenesis and long-term ecosystem development (Stevens and Walker 1970, Walker and Syers 1976, Thompson 1981, Vitousek 2004, Wardle et al. 2004). Despite criticism of the sometimes indiscriminant use of the chronosequence method for understanding vegetation succession (Pickett 1989, Walker and del Moral 2003, Johnson and Miyanishi 2008), we propose that consistent, robust results emerge from a range of chronosequence studies worldwide, at least at the ecosystem level.

In this paper, we refine concepts of ecosystem retrogression to better understand the long-term decline of ecosystem productivity and other ecosystem processes associated with the prolonged absence of rejuvenating disturbances. First, we summarize the body of literature on this topic and identify unifying trends. Next, we evaluate the causes and consequences of retrogression in ecosystems, and develop a new conceptual framework that incorporates ideas developed across disparate disciplines of ecology, biogeochemistry, geology, and soil science. Finally, we evaluate the generality and consequences of these concepts to contrasting ecosystems from around the world in order to catalyze future research.

WHAT IS ECOSYSTEM RETROGRESSION?

Ecosystem retrogression is much less well understood than the progressive and maximal biomass phases of succession. Retrogression is characterized by reductions in ecosystem productivity and standing plant biomass, declines in the availability of nutrients, and shifts in both aboveground and belowground communities to dominance by nutrient-stress-tolerant, slow-growing species (sensu Lambers and Poorter 1992, Grime 2001, Wardle 2002) that are adapted to nutrient poor conditions (Fig. 1). Early studies using pollen analysis in peat or mor soil surface layers in post-glacial deposits showed examples of ecosystems with permanently reduced productivity (Iversen 1964). These so-called retrogressive successions were associated in part with leaching of the soils during pedogenesis, but also with anthropogenic disturbances. Retrogression is frequently associated with the reduced availability of major soil nutrients (particularly phosphorus but also nitrogen; Walker and Syers 1976, Vitousek 2004, Wardle et al. 2004). Thus, the decline in standing biomass that characterizes retrogression occurs because of a long-term reduction in the rate of supply of nutrients limiting to plant growth rather than age-related mechanisms such as declines in physiological processing rates or short-term soil nutrient availability

Fig. 1. Representative photographs illustrating three distinct phases of ecosystem development, progressive (i.e., build-up), maximal biomass, and retrogressive (i.e., decline), for chronosequences including Franz Josef, New Zealand; Cooloola, Australia; Hawaii, USA; and Arizona, USA. Details of these and additional chronosequences having a distinct retrogressive phase are summarized in Table 1. Arizona photo credits: Paul Selmants.

(e.g., Brais et al. 1995, Gower et al. 1996, Ryan et al. 1997, Magnani et al. 2000).

Ecosystem retrogression differs from changes that occur during shorter-term secondary succession and age-related decline in forest productivity in several ways. First, secondary succession is usually initiated by disturbances that need only be sufficiently severe to remove or reduce biomass of primary producers, and that do not necessarily have strong effects on soils or parent substrate. Meanwhile ecosystem retrogression can be reversed only by "rejuvenating disturbances," that is disturbances of sufficient severity to expose new parent material or allow organisms to access otherwise unavailable substrate and nutrients. For example, in regularly burnt systems such as the Cooloola chronosequence in Queensland Australia, each fire may only be of sufficient intensity to induce short-term secondary succession, while in contrast, in less frequently burnt systems such as on forested islands in northern Sweden, fire can be sufficiently severe to remove layers of peat and reverse retrogression (Wardle et al. 2004; Table 1). Second, shorter term secondary succession usually involves one or few generations of dominant plants and their biological interactions (e.g., Huston and Smith 1987, Grime 2001) whereas retrogression usually occurs over much longer time scales that involve many (i.e., dozens or more) generations of dominant plant species and their cumulative influences belowground. As such,

TABLE 1. Summary of intensively studied long-term chronosequences that include distinct retrogressive stages and for which detailed studies have been published.

Chronosequence	Location	Parent material	Disturbance	Age gradient (kyr)	Vegetation	Climate	References
Cooloola	Australia	quartz sand	deposition	0–750	forest	subtropical	Thompson (1981), Walker et al. (1981)
Hawaiian Islands	United States	basalt tephra	volcanism	0–4100	rain forest	subtropical	Vitousek (2004, and refs therein)
San Joaquin Valley	United States	granite	alluvial	0.1–300	grassland	xeric	Harden (1982), Baisden et al. (2002)
Northern Arizona	United States	basalt	volcanism	1–6000	woodland	semiarid	Selmants and Hart (2008, 2010)
Franz Josef	New Zealand	schist, gneiss	glaciation	0–120	rain forest	temperate	Walker and Syers (1976)
Waitutu	New Zealand	mudstone, sandstone	geologic uplift	24–900	rain forest	temperate	Ward (1988), Coomes et al. (2005)
Mendocino	United States	graywacke-sandstone	geologic uplift	100–400	forest	temperate	Jenny et al. (1969), Jenny (1994)
Glacier Bay	United States	sandstone, limestone	glaciation	0–14	forest	boreal	Noble et al. (1984), Chapin et al. (1994)
Swedish islands	Sweden	granite	fire	0–6	forest	boreal	Wardle et al. (1997, 2003)

the time scales involved with shorter-term secondary succession (decades to centuries) are much shorter than those associated with retrogression (millennia), reflecting the relative temporal scale of processes driving these phenomena. Third, although altered soil nutrient availability is one of many mechanisms thought to drive shorter term secondary succession, we suggest that retrogression is ultimately driven by the long-term decline in soil nutrient availability to plants, particularly phosphorus, as a result of pedogenic processes. As such, ecosystem retrogression involves understanding the interplay among biological communities and soil processes over much longer time scales than those that characterize other successions.

Declining nutrient availability is thought to be the ultimate cause of retrogression, and it may be driven by either nutrient depletion or restricted availability. This decline can occur in a number of ways, although the most commonly invoked causes are through leaching of nutrients from the parent material (i.e., either below the rooting zone or exported from the system) or restriction of nutrient supply to plants through chemical transformations that occlude nutrients or produce barriers to nutrient access (e.g., formation of iron, silica, or calcium carbonate pans, or accumulation of exchangeable aluminum to toxic levels; Chadwick and Chorover 2001; Fig. 2). For example, the long-term decline to retrogressive pygmy forest in the classic Mendocino soil staircase chronosequence in California is due to a decline in nutrient availability associated with the formation of soil horizons and waterlogging that restrict root access to nutrients (Jenny et al. 1969, Jenny 1994). Similarly, the retrogressive sequence identified on forested islands in northern Sweden (Wardle et al. 1997, 2003, Lagerström et al. 2007) is driven by the substantial build up of humus physically separating roots from the parent material, thus reducing plant access to rock-derived nutrients. Long-term nutrient declines may be slowed by nutrient inputs or by mechanisms that retain nutrients within the system. For example, retrogression in the Hawaiian Islands chronosequence (Vitousek 2004) involves a decline in forest biomass and stature, but the vegetation does not develop into "pygmy forest" like the latter stage of the Mendocino sequence (Table 1) because there are sufficient inputs of nutrients from atmospheric sources to maintain a moderately tall-statured forest (Chadwick et al. 1999; Fig. 2). Similarly, maintenance of high plant biomass in old and highly weathered soils of the Amazon basin, Southeast Asia, Australia, and south-central Africa is likely due to plant adaptations that retain nutrients within the system (Ashton 1989) as well as atmospheric nutrient inputs (e.g., Okin et al. 2004, Koren et al. 2006, Boy and Wilcke 2008).

Aspects of ecosystem retrogression have been studied by researchers in different scientific disciplines, such as ecology, biogeochemistry, geology, and pedology. However, these groups have developed their conceptual frameworks somewhat independently (but see Walker et al. 1981, Vitousek 2004). Therefore the available information on retrogression is dispersed through a broad spectrum of the scientific literature. A general conceptual model of ecosystem retrogression that draws on these areas of expertise is needed in order to shed light on the diverse causes and consequences of ecosystem retrogression. This need for an interdisciplinary approach arises because the rates of primary productivity and other ecosystem processes are constrained by nutrients derived from both atmospheric sources (e.g., N and P deposition; cations in dust) and parent substrate-derived elements (e.g., P and cations), and are therefore controlled by both biological and geological processes (Chadwick et al. 1999). We suggest that retrogression should be defined as the depletion or reduction in access to these nutrients by plants and other organisms that slows ecosystem process rates to such a level that standing plant biomass and the functioning of other biota are substantially impaired; these processes can only be reversed via rejuvenating disturbance that resets the system (e.g., glaciation, volcanic activity, landslides), or stabilized by changes in other external factors such as atmospheric inputs, appropriate nutrient subsidies or changes in fire regime.

BRIEF PROFILE OF RETROGRESSIONS AROUND THE WORLD

Long-term chronosequences provide a model system for testing ideas about ecosystem development generally, and retrogression in particular (Vitousek 2004, Wardle et al. 2004). As such, they contribute to the development of general principles about the extrinsic factors that regulate community and ecosystem properties and processes, both above and below ground. In particular, these include the roles of soil nutrient limitation, species adaptations and historic disturbance regime (Walker and Syers 1976, Wardle et al. 1997, Vitousek 2004, Coomes et al. 2005, Selmants and Hart 2008). These drivers operate on a range of temporal scales, but it is the cumulative effects of these processes and their influence on very long-term processes such as pedogenesis that distinguishes retrogression from shorter-term successional pathways. A number of long term seres worldwide that include retrogressive stages have now been characterized, notably in New Zealand, Hawaii, Alaska, the contiguous USA, Australia, and Sweden (Table 1); these sequences represent vastly differing bioclimatic, parent material, and rejuvenating disturbance that initiated the chronosequence. Collectively, these chronosequences demonstrate that ecosystem properties and processes follow somewhat predictable long-term trajectories of decline across contrasting systems (summarized in Table 1, Fig. 1), and that ecosystem retrogression is not a system-specific phenomenon but occurs on a range of parent substrates, vegetation types and climatic zones (Table 1). The rate at which retrogression occurs varies widely among systems, suggesting that key drivers or their relative importance differ among sites, but despite this variation, the eventual consequences of retrogression are similar (Wardle et al. 2004, Vitousek et al. 2010). Finally, ecosystem retrogression results from interactions among biogeochemical processes and cycles involving belowground biota and vegetation, implying that feedbacks between the aboveground and belowground components of ecosystems have a major influence in regulating rates of retrogression. The abiotic and biotic changes that underpin ecosystem retrogression are explored and synthesized below.

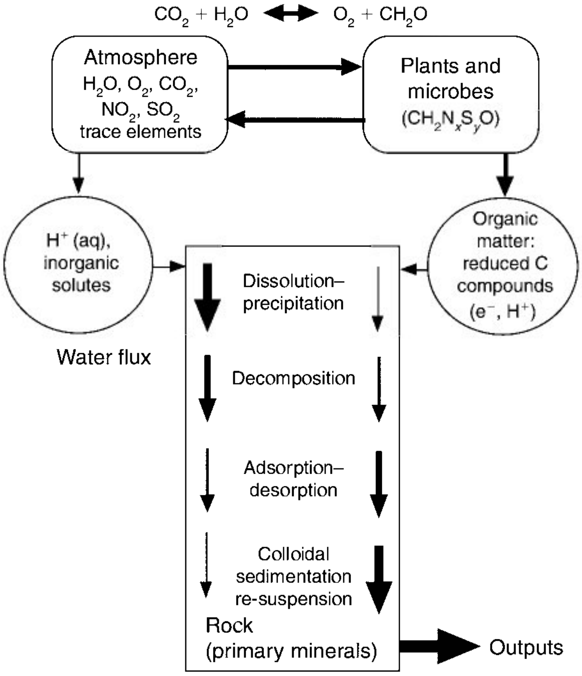

FIG. 2. Atmospheric, biological, and geological interactions controlling soil nutrient availability (redrawn and modified from Chadwick and Chorover [2001]). Acids from the atmosphere and biosphere weather rocks that release nutrients as well as elements that precipitate into oxides that can retain nutrients in available or non-available forms; depletion of the primary mineral store and accumulation of oxides can cause retrogressive processes to dominate. Atmospheric addition of mineral dust can retard ecosystem retrogression by adding fresh nutrients to the biologically active surface layers of soil. Arrow direction and thickness illustrate the magnitude and direction of processes governing nutrient fluxes. Outputs are losses to the system controlled by atmospheric inputs, and biological and physical processes. The role of organically bound forms of N and P dominates during ecosystem retrogression (Walker and Syers 1976, Turner et al. 2007).

CAUSES, CONSEQUENCES, AND MECHANISMS

The drivers of ecosystem retrogression involve three interlinked components that operate at different temporal scales that collectively regulate the rate and magnitude of ecosystem retrogression through their influences on both soil processes and biological communities (Vitousek 2004, Wardle et al. 2004). First, nutrient limitation is maintained and exacerbated over the long term through outputs exceeding inputs (in the order of millennia and beyond). Second, resource limitation to biological processes occurs through demand exceeding supply (over the order of days to weeks). Third, biological responses to these limitations result in the development of resource sinks through mechanisms such as high nutrient-use efficiency (NUE), lower quality and decomposition rates of plant litter, and accumulation of nutrients in plants (in the order of months to centuries). We now discuss how these drivers interact to control ecosystem processes and retrogression through feedbacks involving biological processes both above and below ground, as well as their long-term links to pedogenesis.

Long-term sources and sinks of nutrients

The best-characterized driver of retrogression is the reduced availability of parent substrate-derived nutrients during long-term pedogenesis, which may arise through several mechanisms. Over thousands to millions of years, the loss of parent substrate-derived nutrients is an inevitable consequence of weathering and soil development (Jenny 1994), although the rate at which this occurs is likely to be highly dependent on climate (Chadwick et al. 2003, Porder and Chadwick 2009). The action of rain water, exudation of organic acids by plants, hyphae of mychorrhizal fungi, and physical disturbance cause the breakdown of primary minerals in bedrock through chemical weathering (Chadwick and Chorover 2001). As these minerals dissolve, P and cations are lost by leaching and runoff, especially as soil exchange sites either diminish via shifts in soil mineralogy or are filled by hydrogen (H) and aluminum (Al) ions during soil acidification (e.g., Lichter 1998). Phosphorus, though substantially less mobile than cations, can also be lost through leaching (Turner and Haygarth 2000), and in addition can be transformed into bound forms that are believed not to be readily available for plant uptake (Walker and Syers 1976, Turner et al. 2005, 2007). Replenishment of these minerals occurs only through deposition or erosion, both of which may be continuous, semi-continuous, or instantaneous.

Mineralogical changes that occur during soil development are a key cause of declines in nutrient availability and ecosystem retrogression. Apatite, the main primary P mineral in most parent substrates, is relatively soluble, and in acid or humid systems is largely dissolved over the course of the first few thousand years of pedogensis (Walker and Syers 1976, Crews et al. 1995, Vitousek et al. 1997). In addition to uptake by biota and removal by drainage or erosion, inorganic P released from primary mineral dissolution is reversibly absorbed onto the surfaces of iron and aluminum oxides formed during soil weathering. Therefore, in the early and intermediate stages of soil development, abiotic P supply is controlled by a combination of primary mineral dissolution and adsorption-desorption reactions associated with secondary minerals (Tiessen 2005). However, with time, the inorganic P adsorbed on oxide mineral surfaces becomes occluded and less readily desorbed due mainly to a combination of solid-state diffusion of P into the mineral structure and deposition of new minerals on oxide surfaces (Barrow 1983). The physicochemical occlusion of adsorbed P, together with formation of recalcitrant P minerals by reaction with iron, aluminum and calcium released during weathering, significantly reduces the bioavailability of inorganic P during the advanced stages of soil development (Adams and Walker, 1975, Cross and Schlesinger 1995, Tiessen 2005, Turner et al. 2007). These processes operate over longer time scales than those processes controlling soil nutrient availability during shorter-term secondary successions and age-related changes in forest communities.

On silica-rich (felsic) substrates such as granite, sandstone, and schist, soil mineralogy in humid climates progresses from quartz–feldspar–mica assemblages to dominance by iron oxides, gibbsite, and kaolinite, with the quartz dissolving from some highly weathered soils (Lucas et al. 2003). On silica-poor, base-cation-rich (mafic) substrates such as basalt and gabbro, plagioclase-pyroxene-dominated parent materials may progress to ferrihydrite–allophane–imogolite and, after hundreds of thousands of years, to kaolinite–geoethite–hematite assemblages (Kurtz et al. 2001). In both cases, these mineralogical shifts lead to decreased cation retention in subsoils, and increased binding of the remaining P in relatively recalcitrant forms. Furthermore, rock types vary greatly in their initial P content; some sandstones contain as little as 40 ppm P and basalts can have 4000 ppm P whereas continental crust contains about 700 ppm (Taylor and McClennan 1985). Although there is a paucity of data on this topic, it appears that the rate of P loss can vary across rock types, i.e., up to 10-fold faster on basalt compared to granite in similar climates (Porder et al. 2007), and five-fold with increasing rainfall on the same parent material (Walker and Syers 1976, Porder and Chadwick 2009). It is premature to generalize these findings; further research is needed to determine the functional form of these relationships, and the bioavailability of P from various pools in the soil (Richter et al. 2006).

A common aspect of the pedogenic changes in soil P during retrogression is its accumulation in organic and occluded forms, which can eventually represent most of the total soil P (Syers and Walker 1969, Parfitt et al. 2005, Turner et al. 2007); however, this pattern of change is not universal (Lagerström et al. 2009). The accumulation of organic P is rarely assigned any ecological significance because models that describe changes in P during pedogenesis consider organic P as a single functional pool of limited availability to plants (Walker and Syers 1976; but see Turner 2008). However, soil organic P occurs in a broad spectrum of compounds in forest soils which vary greatly in their availability to organisms (Attiwill and Adams 1993, Condron et al. 2005). Although little information is available on the changes in organic P forms during the retrogressive phase, a recent study of the Franz Josef chronosequence revealed that losses of amorphous oxides and accumulation of organic matter during this phase appeared to favor the depletion of the inositol phosphates, which are to be stabilized by association with metal oxide surfaces and the retention of compounds such as DNA, perhaps bound within large, recalcitrant humic molecules rather than the inositol phosphates, which appear to be stabilized by association with metal oxide surfaces (Turner et al. 2007). This is surprising, because compounds such as DNA are conventionally considered relatively labile in soils, yet they persist under retrogressive forests that have significant P limitation, perhaps indicating an additional mechanism by which P availability declines in retrogressive stages of chronosequences. In contrast, inositol phosphates declined markedly in older soils, which may be linked to the increasing crystallinity of metal oxides (and therefore weaker stabilization) in later stages of pedogenesis (Celi and Barbaris 2007, Turner et al. 2007).

The depletion of parent substrate-derived nutrients can be measured by comparison to relatively immobile elements (Brimhall et al. 1988, Kurtz et al. 2000), and during long-term pedogenesis external sources of "rock-derived" nutrients can become increasingly important for ecosystem production. For example, immobile element analysis at the 4.1 million year old (ma) stage of the Hawaiian Islands chronosequence has revealed that more than 4 m of rock has weathered to form 1 m of soil (Vitousek 2004). Of the total P in the 4.1 ma site, over 90% has been derived from atmospheric sources, so the depletion of parent material is even more extreme than appears from concentration data alone (Vitousek 2004). Plant strontium isotopes indicate that ~90% of Sr (and by proxy, Ca) in leaves at the oldest sites is derived from atmospheric sources (Kennedy et al. 1998, Chadwick et al. 1999). These results highlight two points: first, chronosequences provide unparalleled information on long-term environmental controls over nutrient loss and sequestration, and second, nutrient inputs or subsidies are important for maintaining the long-term productivity of systems and slowing the development of retrogressed ecosystems. Thus, drivers of both nutrient inputs and outputs determine long-term ecosystem processes and properties.

It is reasonable to assume that in the absence of rejuvenating disturbance, plant productivity in undisturbed systems will continue to decline with time as net P loss from the plant root zone continues, and will only stabilize when the rate of P loss from the root zone is either equal to or less than the rate of exogenous P input. The availability of P to plants in retrogressive systems is primarily determined by the balance of P flux between the organic P, plant P, microbial P, and litter–biomass P pools; this is based on the assumption that occluded forms of inorganic P are effectively not bioavailable (Walker and Syers 1976, Condron et al. 2005; but see Richter et al. 2006). There is some evidence from microcosm studies that occluded forms of P may in fact be bioavailable (e.g., Gahoonia and Nielsen 1992, Chen et al. 2002); however, the importance of occluded P for maintaining biological processes in natural ecosystems is not known. Atmospheric P inputs are sometimes ignored in the context of ecosystem P dynamics (but see Okin et al. 2004, Pett-Ridge 2009), but they are likely important in stabilizing the productivity of retrogressive systems (Chadwick et al. 1999, Hedin et al. 2003). Ultimately the long-term P status in ecosystems is a balance of loss and occlusion balanced by exogenous and parent-material derived inputs, but these fluxes have rarely been documented in retrogressed ecosystems (but see Vitousek 2004).

It is also apparent that the nature of inputs of P and N differ from each other throughout ecosystem development, including during retrogression. Since P is derived from mineral dissolution, once this source is effectively exhausted only tight recycling and exogenous inputs can sustain ecosystem processes in the long term. Further, the rate at which an ecosystem approaches this terminal steady-state condition (i.e., where outputs are balanced by exogenous inputs) should be heavily influenced by the rate of dust input. For example, in Hawaii, where dust fluxes are amongst the lowest in the Northern Hemisphere, the process takes millions of years (Vitousek 2004). In contrast, N is largely absent from parent materials but quickly builds up via root-associated and free-living biological N fixation early in the progressive phase of ecosystem development. However, this N fixation is not necessarily restricted to the progressive phase. For example, some biological N fixation has been shown to occur in association with lichens, bryophytes, and leaf litter during retrogression in both the Hawaiian (Crews et al. 2000, Matzek and Vitousek 2003) and Franz Josef (Menge and Hedin 2009) chronosequences. Further, in the Swedish islands sequence, N fixation by cyanobacteria associated with mosses increases as retrogression proceeds, with N input from this source eventually exceeding N input from rainfall (Lagerström et al. 2007). This N fixation by mosses appears to be governed by interactions with vascular plants that become more important as retrogression proceeds (Gundale et al. 2010). Similarly, in the Cooloola sequence, shrub species that form root nodules containing N-fixing bacteria occur commonly during retrogression (Wardle et al. 2004).

Long-term depletion of P during retrogression along with some replenishment of N commonly leads to P rather than N limitation, and this is supported through several lines of evidence. First, fertility studies associated with soil mapping in California rangeland and cropland found increasing P limitation of crop plants as retrogression occurred, in a manner consistent with modern studies (Baisden et al. 2002). For example, Herbert and Fownes' (1995) fertilizer experiment in the Hawaiian chronosequence demonstrated that P rather than N limits tree productivity during retrogression. Similarly, bryophyte N fixation is greatly enhanced by the addition of P only in the late stage of the Hawaiian chronosequence (Benner et al. 2007). In addition, there is evidence from contrasting chronosequences worldwide for increasing N to P ratios of both litter and humus during retrogression (Wardle et al. 2004, 2009; see also Ostertag 2010). However, N availability can also decrease during retrogression because N can be bound in plant litter and humus in increasingly unavailable forms (e.g., in polyphenolic complexes); evidence for this has been found both for the Mendocino staircase sequence

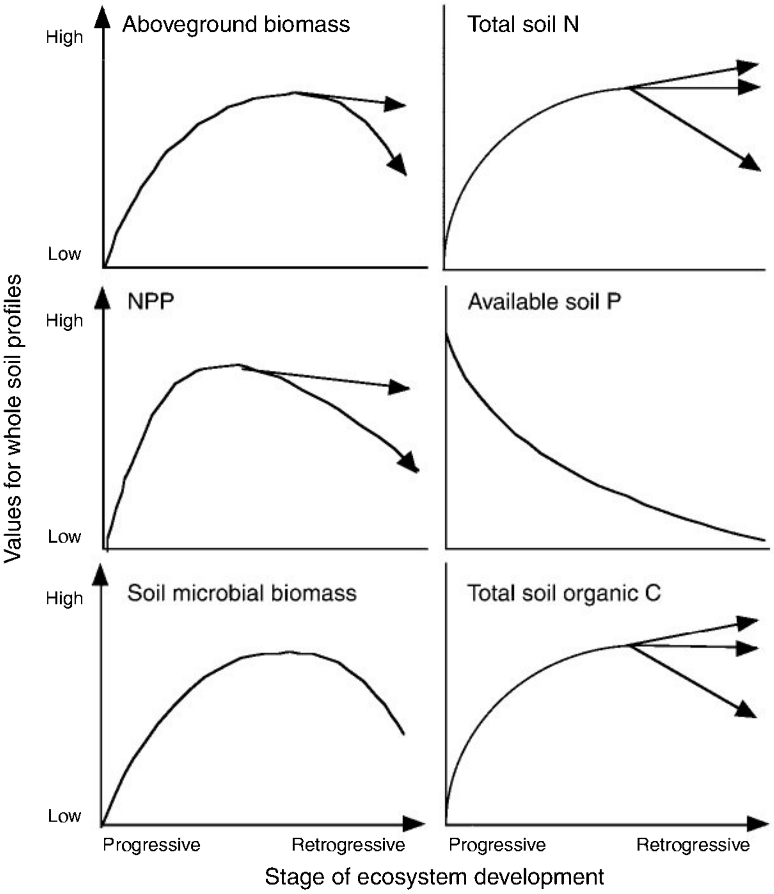

FIG. 3. Summary of expected changes in ecosystem properties throughout ecosystem development, including retrogressive stages. Time to stage of ecosystem development varies widely among sites, but the overall patterns appear to be robust. Multiple arrows for expected changes during the retrogressive phase reflect variation in the magnitude and direction of changes during retrogression observed among intensively studied chronosequences (Table 1). NPP is net primary productivity; *y*-axes data are relative values for whole soil profiles.

(Northup et al. 1995), and for the Swedish lake island sequence (Wardle et al. 1997). This is also supported by ^{15}N stable isotope analyses of plant and soil material from both the Swedish island chronosequence (Hyodo and Wardle 2009) and the northern Arizona sequence (Selmants and Hart 2008), which points to more conservative N cycling during retrogression. These shifts to recalcitrant forms of N during retrogression can be independent of or secondary to P limitation. More generally, N and P behave very differently in soils in that accretion of soil N will not result in the long-term storage of N if inputs are reduced because N is lost so easily whereas P added to the system is more likely to persist, but is transformed within the system in such a way that P availability is reduced. Thus, the trajectories of N and P availability differ throughout ecosystem development (Fig. 3), which is important in determining both the N:P stoichiometry of the system and the relative role of N and P in controlling net primary production (NPP; see also Ostertag 2010, Vitousek et al. 2010).

Plant functional traits and community attributes

Plant species and communities show predictable shifts in functional traits early in ecosystem development (Grime 2001, Eviner and Chapin 2003, Walker and del Moral 2003, Richardson et al. 2004), but the issue of how functional traits change during retrogression is relatively unexplored. We predict that as ecosystem development proceeds from the progressive phase to the maximal biomass phase and finally to the retrogressive phase, the dominant plant species should shift generally from fast-growing, short-statured species to tall, slower-growing, dominant species, and finally to long-lived, slow-growing species, analogous to Grime's (1977, 2001) continuum of ruderal-competitive-stress-tolerant plant species. In contrast to studies of plant trait changes during shorter-term secondary successions involving one or few plant generations, ecosystem retrogression occurs over a much longer time scale that involves dozens to hundreds of generations of the dominant plant species. This has several important implications. For example, intraspecific variation in traits through species adjustment to declining nutrient availability during retrogression (Richardson et al. 2004, Wardle et al. 2009) is more likely to influence ecosystem properties through long-term interactions among species and with soil processes. In addition, functional traits relating to different nutrient uptake strategies by plants and associated mutualists become particularly important during ecosystem retrogression (e.g., Lambers et al. 2008, Dickie and Holdaway 2010).

Shifts in functional plant traits (other than foliar nutrient concentrations) during retrogression have been described most comprehensively from the Franz Josef (Richardson et al. 2005, Turnbull et al. 2005, Whitehead et al. 2005) and Hawaiian Islands (Joel et al. 1994, Cordell et al. 2001) chronosequences. For example, in the Hawaiian Islands chronosequence, leaf size of the dominant tree (*Metrosideros polymorpha*) increases through the progressive phase and decreases during the retrogressive phase, whereas leaf thickness decreases during the progressive phase and increases during retrogression (Cordell et al. 2001). Meanwhile, for the Franz Josef chronosequence, leaf size declines but leaf density (g/cm^3) and thickness increases during retrogression across all woody species, largely because of the increasing relative dominance of podocarps over angiosperms during retrogression (Richardson et al. 2004; S. Richardson and D. Peltzer, *unpublished data*). Further, leaf mass per unit area (LMA) increases as nutrient availability declines during retrogression both for *M. polymorpha* in the Hawaiian Islands chronosequence (Vitousek 1998, Cordell et al. 2001), and for various species across the Franz Josef chronosequence (Whitehead et al. 2005). Foliar and leaf litter N and P concentrations frequently decline from peak biomass to retrogressive stands, but nutrient resorption (notably for P) becomes more proficient (Crews et al. 1995, Vitousek et al. 1995, Vitousek 1998, Richardson et al. 2004, 2005). Cordell et al. (2001) reported that leaf longevity of *M. polymorpha* was less on a 300-year-old aggrading site than on a 4.1-million-year-old retrogressive site in Hawaii. Also, stand-level measurements by Herbert and Fownes (1999) showed a decline in leaf longevity from young aggrading to peak-biomass stands, followed by an increase into older stands. Consistent with this, in the Swedish island system, deciduous species with fast leaf turnover become less abundant during retrogression while species with long-lived leaves and slow tissue turnover increasingly dominate (Wardle et al. 2003, Wardle and Zackrisson 2005). Leaf-level traits reflecting structural adjustments to reduced nutrient availability thus follow broadly predictable patterns during retrogression.

Changes in leaf quality are reflected in function. For example, the maximum rate of photosynthesis ($A_{\max}$) per unit leaf area declines during retrogression across dominant tree species (Cordell et al. 2001, Whitehead et al. 2005), as do rates of dark respiration and respiration at 25°C (Turnbull et al. 2005). However, declines in photosynthesis and respiration are not proportional: the ratio of $A_{\max}$ to R_{d} declines with site age, indicating that the cost of photosynthesis increases during retrogression (Turnbull et al. 2005). Shifts in plant species composition may account for many of these leaf-level shifts along chronosequences, but similar shifts in leaf function and traits also occur within species (Cordell et al. 2001, Richardson et al. 2005). These data support well established ideas that leaf traits are tightly coupled and that shifts in one trait result in concomitant or compensatory shifts of other traits (e.g., Grime et al. 1997, Díaz et al. 2004, Wright et al. 2004). For example, foliar and litter nutrient concentrations responded very strongly to retrogression along the Franz Josef and Hawaiian chronosequences. Coupled shifts were most commonly seen for foliar N and $A_{\max}$. Little is known about changes in root traits along chronosequences or their linkage with aboveground changes, thus, plant community attributes shift in broadly predictable ways during retrogression to dominance by a set of stress-tolerant species characterized by low foliar nutrient concentrations, high leaf tissue density, and reduced rates of physiological processes.

Community-level characteristics such as species richness and diversity are less consistently responsive to ecosystem retrogression than are functional traits, but may also shift during retrogression. As retrogression proceeds, aboveground biomass and NPP are reduced while the proportion of belowground biomass increases (Walker et al. 1987, Crews et al. 1995, Kitayama and Mueller-Dombois 1995, Wardle et al. 2003). Understory plant diversity either remains constant or increases during retrogression while tree diversity often declines; these shifts are not strongly associated with shifts in aboveground biomass of the dominant plant species (Crews et al. 1995, Kitayama and Mueller-Dombois 1995, Wardle et al. 2008*a*). How species interactions shape this pattern of distribution and abundance is poorly understood. However, if retrogression is viewed as a special case of increasing environmental stress (Grime 2001), then a shift from facilitation very early in succession, to strong competitive interactions at the maximal biomass phase, to weak competitive (or even facilitative) interactions during retrogression might be expected. In partial accordance with this, manipulative experiments performed across the Swedish islands chronosequence show that during retrogression, there is a decline in the intensity of interspecific competitive effects of dwarf-shrub species on each other (Wardle and Zackrisson 2005) and on the establishment of tree seedlings (Wardle et al. 2008*b*), although their effect on moss biomass may actually increase (Gundale et al. 2010). Much remains unknown about how emergent community properties such as species composition and diversity depend on stage of ecosystem development, or other processes such as assembly history and species pool availability (Pärtel 2002, Fukami 2004, Fukami et al. 2005).

Responses of belowground and aboveground consumers

The quantity and quality of resources that plants produce are important determinants of consumer organism abundance and composition (Coley et al. 1985, Wardle 2002). The abundance or biomass of consumer organisms should generally decline during retrogression as the availability of their food resources declines. In the belowground food web, the primary consumers are microorganisms (bacteria and fungi). Several studies have shown that during the progressive phase of ecosystem development, soil microbial communities show strong, largely predictable shifts in composition and activity (e.g., Ohtonen et al. 1999, Tscherko et al. 2003, Bardgett et al. 2007), but much less is known about microbial responses to the retrogressive phase. Several studies have shown that total biomass and respiratory activity of the soil microflora generally decline during retrogression, in tandem with plant biomass (Wardle and Ghani 1995, Wardle et al. 1997, Williamson et al. 2005, Lagerström et al. 2009; Fig. 3). Further, the study of Wardle et al. (2004) considered the response of microbial community structure to ecosystem retrogression for six contrasting chronosequences worldwide and found that retrogression was matched not just by declines in microbial biomass, but also by shifts in the composition of microbial communities towards increasing fungal dominance. This shift is also consistent with increasing soil acidification that often occurs during ecosystem development, in that acidic soils ($pH < 5$) are typically fungal-dominated (van der Heijden et al. 2008), and are usually associated with reduced rates of litter decomposition and mineralization of nutrients (Hobbie and Vitousek 2000, Wardle et al. 2003, 2009). These findings suggest that increasing P limitation during retrogression sets a positive feedback in motion whereby low foliar and leaf litter nutrient status alters microbial community structure, reduces overall decomposer activity, and further intensifies nutrient limitation and accelerates retrogression (e.g., Fig. 4 in Vitousek 2006). We expect that changes in root tissue quality should also drive this feedback, but this idea remains to be tested.

Particular functions performed by the soil microbial community may be highly responsive to retrogression. For example, Allison et al. (2007) found increasing microbial phosphatase activity, and decreasing activity of C- and N-hydrolyzing enzymes through the retrogressive stages of the Franz Josef chronosequence. This was taken to be indicative of increasing limitation of the microbial community by P rather than C, and increasing microbial investment in P acquisition from organic P sources. Strong correlations between microbial community composition and P availability make it difficult to determine whether changes in enzyme activity are due to shifts in nutrient availability or in microbial community composition. Further, Olander and Vitousek (2000) and Treseder and Vitousek (2001) provide evidence for N limitation of phosphatase production in retrogressed sites in Hawaii. Such results indicate increasing P limitation of the soil microbial community, and thus provide supporting evidence of the importance of interactions between microbes and nutrient availability in retrogressive ecosystems.

Mycorrhizal communities are commonly thought to shift from dominance by non-mycorrhizal, to arbuscular myrcorrhizas to ericoid or ectomycorrhizal species during succession or ecosystem development (Read and Perez-Moreno 2003, Lambers et al. 2008). However, plants that occur on retrogressive stages can be associated with arbuscular mycorrhizas (e.g., *Metrosideros* species in Hawaii and New Zealand, *Eucalyptus* species in Australia), ectomycorrhizas (e.g., *Picea abies* in Sweden and *Nothofagus solandri* in New Zealand, *Eucalyptus* species in Australia) or ericoid mycorrhizas (e.g., ericaceous dwarf shrubs in Alaska and Sweden). Similarly, dominant tree species in tropical forests that have low soil P can be arbuscular mycorrhizal (e.g., Araucariaceae in the Pacific and South America, Podocarpaceae), ectomycorrhizal (e.g., Dipterocarpaceae, Caesalpinioideae) or non-mycorrhizal (e.g., Proteaceae, Santalaceae) (Högberg 1986, Andrade et al. 2000, Brundrett 2009). Therefore, the simple expectation of a distinct transition to ectomycorrhizal dominance during retrogression is not strongly supported by data or observations (Dickie and Holdaway 2010). In addition to mycorrhizal mutualists, there are also physiological and morphological adaptations of roots to very low soil nutrient availability, such as those that plants encounter during retrogression. For example, cluster or dauciform roots are specialised adaptations for increased uptake of P in extremely nutrient-poor conditions (Lambers et al. 2008). Similarly, shallow root mats in some tropical forests allow for direct nutrient transfer from decomposing litter to roots, thus short-circuiting nutrient cycling (Herrera et al. 1978, Stark and Jordan 1978). Further, some plants and soil microbes that can access complex soil organic P compounds, for example through the synthesis of phytases, secretion of organic acids or association with mycorrhizal fungi adapted to access soil organic P may be favored at older stages of ecosystem development (Turner et al. 2007). It is also recognized that similar processes probably operate in low-fertility systems more generally (Read and Perez-Moreno 2003, Lambers et al. 2008). The costs and benefits associated with these different strategies for acquiring nutrients and their relative importance are poorly understood, but retrogressive ecosystems are ideal systems for testing hypotheses on this topic (Treseder and Vitousek 2001, Lambers et al. 2008).

Soil microbes form the basal consumer level of the soil food web, which also includes soil animals that feed primarily on microbes and on each other (Lavelle 1997). Although several studies have considered how soil fauna respond to ecosystem progression (e.g., Hodkinson et al. 2001, Kaufmann 2001), few have considered soil faunal responses to retrogression. Williamson et al. (2005) found densities of microbe-feeding and predatory nematodes to decline during retrogression in the Waitutu chronosequence of New Zealand. These authors also found the ratio of fungal-feeding to bacterial-feeding nematodes to increase, indicative of multitrophic consequences of increasing dominance by fungi during retrogression. Meanwhile, Doblas-Miranda et al. (2008) found that along the Franz Josef chronosequence, the abundance of several groups of soil and litter dwelling microfauna and macrofauna (representing several trophic levels) demonstrated a unimodal relationship with ecosystem stage, and all declined sharply during retrogression. Conversely, Jonsson et al. (2009) found few consistent responses of soil nematodes, mites, and springtails to retrogression for the Swedish island chronosequence. Given the role of soil fauna in regulating decomposition and nutrient cycling processes, substantial reductions in the densities of soil animals during retrogression are likely to contribute further to reduced nutrient availability during retrogression.

The issue of how aboveground consumers (herbivores and their predators) respond to retrogression has seldom been explored. Gruner (2007) found for the Hawaiian Islands chronosequence that the densities and diversity of foliar herbivores and predators in the canopy of *Metrosideros polymorpha* generally peaked at intermediate chronosequence stages and declined during retrogression. This may be a consequence of shifts in foliar quantity and quality, or alternatively reflect shifts from qualitative to quantitative defense, although this has not been explored. In contrast, on the Swedish islands chronosequence, Crutsinger et al. (2008) found that the dominant herbivore of *Betula pubescens* (the weevil *Deporaus betulae*), and foliar damage by the herbivore, increased during retrogression despite foliage being of poorer quality and more heavily defended. They suggested that the weevils were utilizing defense compounds in the foliage of plants on retrogressive islands for their own defenses. Subsequent studies on this system have also found predators such as spiders and beetles to have a greater abundance on islands that had undergone retrogression (Jonsson et al. 2009), and for stable carbon isotope ratio values of spider tissue to decline together with values for leaves and soil during retrogression (Hyodo and Wardle 2009). Such results are indicative of retrogression exerting a multitrophic effect on invertebrate food webs.

Aboveground and belowground linkages: implications for ecosystem processes

The large changes that occur in both aboveground and belowground communities during retrogression are likely to be driven in part by feedbacks between the vegetation, soil biota and belowground processes. It has been proposed that negative feedbacks may be of limited importance during initial stages of succession because the necessary drivers such as host-specific pathogens are typically absent (Reynolds et al. 2003). However, as plant host densities increase and soil profiles develop during ecosystem development, the environment for pathogens likely improves, thereby increasing the scope for negative feedback to occur (van der Heijden et al. 2008). Further, the scope for positive feedback should also increase, through the development of both host-specific mycorrhizal communities (Selosse et al. 2006), and microbial communities that preferentially mineralize litter of the dominant plant species (Vivanco and Austin 2008, Ayers et al. 2009). Although the importance of positive or negative biological feedbacks during retrogression has yet to be explicitly and directly tested, the tight linkages between shifts in aboveground and belowground subsystems that occur across retrogressive chronosequence sites points to the likely importance of feedback mechanisms between these subsystems (see Vitousek 2006).

Belowground shifts in dominant energy flows and nutrient cycling processes that are controlled by the soil decomposer community are often strong and predictable across chronosequences. During the progressive stage of ecosystem development, increases in the abundance, activity, and complexity of decomposer communities positively feed back to the plant community through increases in rates of nutrient recycling, particularly of N (Bardgett et al. 2005). Further, a shift from bacterial- to fungal-based energy channels in soil food webs during retrogression (Wardle et al. 2004, Williamson et al. 2005) is likely associated with more efficient and less open nutrient cycling, leading to greater retention of nutrients in the system. As retrogression is approached, soil microbial abundance and activity generally declines, and this is associated with declining availability of N and P in the soil; impairment of these processes can precede declines in the height, biomass, and foliar nutrient concentrations of plant species (Wardle et al. 2003). This could result in belowground regulation of aboveground ecosystem properties during retrogression (Cordell et al. 2001, Wardle et al. 2003, Richardson et al. 2004). Wardle et al. (2004) suggested a feedback mechanism during ecosystem retrogression whereby as ecosystems develop they become increasingly P limited, setting a positive feedback in motion so that low foliar and litter nutrient status reduces decomposer activity, thereby further intensifying nutrient limitation (e.g., Hobbie and Vitousek 2000, Vitousek 2006). The accumulation of nutrients in biomass or recalcitrant organic matter may also promote nutrient limitation in retrogressed ecosystems as discussed above, though it should be noted that to date fertilization experiments to directly test for nutrient limitation during retrogression on a chronosequence have only been performed in the Hawaiian Islands (Vitousek and Farrington 1997).

Changes in aboveground ecosystem properties mirror those belowground. The loss of parent-substrate-derived nutrients during pedogenesis drives plant trait adaptations that act as positive feedbacks to low soil nutrient availability, such as high NUE, long leaf span, high LMA (leaf mass per unit area), and high levels of quantitative defensive compounds (Hättenschwiler and Vitousek 2000, Wardle 2002, Vitousek 2006). These traits are all associated with poor quality litter that breaks down slowly (Swift et al. 1979, Cornwell et al. 2008). Declines in litter quality during retrogression promote more stress-tolerant soil biota, which further slows nutrient cycling through lower soil microbial activity, and the creation of more recalcitrant or organically bound compounds that further diminish nutrient availability (Northup et al. 1995, Turner et al. 2007). Although such feedbacks have been described for relatively short-term successional processes (e.g., Kulmatiski et al. 2008), they also operate over longer time scales of ecosystem retrogression. Hence, long-term changes in ecosystem processes during retrogression are driven by the shorter-term feedbacks between aboveground and belowground communities involving both C and nutrients. These linked shifts in both aboveground and belowground processes, and feedbacks between them have important implications for ecosystem C storage during retrogression. Soil C accumulation occurs during the build up phase of succession, taking up to 10 kyr to reach a quasi steady state (Schlesinger 1990, Harden et al. 1992), but can either continue to increase during retrogression or decline (Figs. 3 and 4). In subtropical Hawaii, noncrystalline minerals derived from volcanic rocks prolong peak soil C storage for in excess of 100 kyr (Torn et al. 1997). In summer-dry California grasslands, C storage in soils formed on granitic alluvium more typical of continental crust reaches a lower steady state at between 40 and 100 kyr (Baisden et al. 2002).

Summary of causes, consequences and mechanisms

Several principles regarding retrogression emerge from the chronosequence studies outlined above. First, plant biomass and NPP both decline during retrogression, but the magnitude of this decline depends on the ratio of nutrient inputs to outputs, and is therefore controlled both by internal nutrient cycling and external drivers (e.g., nutrient deposition or subsidies). Ultimately the long-term P status in ecosystems is a balance of loss and occlusion balanced by exogenous and parent-material derived inputs, but these fluxes have rarely been documented in retrogressed ecosystems. Second, further research is needed to determine the bioavailability of supposedly recalcitrant forms of N and P during ecosystem retrogression. Third, long-term pedological changes can alter hydrological processes, sometimes creating impermeable pans or strata that promote waterlogging or prevent plants from accessing nutrients below them (e.g., Jenny et al. 1969, Thompson 1981, Ward 1988). The end point vegetation of retrogression can thus be relatively high biomass open forest (e.g., Hawaii, Swedish islands), pygmy forest (e.g., Mendocino sequence, Franz Josef, Waitutu), shrubland (e.g., Cooloola, northern Arizona) or sparse shrub–herb fields (e.g., San Joaquin Valley). Fourth, predictable changes occur during retrogression for both aboveground and belowground communities, and for traits of aboveground and belowground organisms, highlighting that the pedogenic changes that occur during retrogression (and resultant nutrient limitation) are major temporal drivers of biota on both sides of the aboveground-belowground interface (Wardle 2002, Bardgett et al. 2005). Fifth, P cycling controls many ecosystem processes either directly or through interactions with C and N, and is controlled in turn through feedbacks involving the biota and pedogenic processes. Finally, in addition to biological processes, explicit inclusion of long-term pedological and physical processes is necessary for understanding the causes and consequences of ecosystem retrogression (Fig. 2).

GENERALITY OF ECOSYSTEM RETROGRESSION

Retrogression in contrasting regions

All of the chronosequences examined in this review show diminished vegetation biomass, nutrient (notably P) availability and other retrogressive properties at the oldest sites. The overall patterns of retrogression are relatively similar across biomes even though the speed and magnitude of retrogression vary among sites, and different drivers and mechanisms are involved. For example, P depletion is profound at the oldest Hawaiian site, and this low P availability is reinforced through feedbacks involving P limitation of primary productivity, plant physiological processes (e.g., declining rates of photosynthesis and respiration), and litter quality (Vitousek and Farrington 1997, Vitousek 2004). In addition, a clay-dominated layer inhibits water infiltration in these soils that may further reduce P availability (Lohse and Dietrich 2005). The sand dunes of Cooloola also show the mineralogical characteristics of nutrient depletion through the formation of giant humus podzols (Thompson 1981). In contrast, retrogression on the Swedish islands chronosequence is driven by the development of a deep humus profile that locks up nutrients and prevents tree roots from reaching the bedrock (Wardle et al. 1997, 2004). The other chronosequences are less easy to diagnose with the available data. The oldest sites at Franz Josef and Waitutu are terraces that are covered with quartzo-feldspathic loess that was probably already depleted in P when the loess accumulated, although this P limitation has certainly been accentuated during retrogression. Further, the presence of relatively unweathered parent material at ca. 1 m depth at the oldest Franz Josef site suggests that the depletion of rock-derived nutrients may not be the sole cause of retrogression there (S. Porder, *personal observation*). The Mendocino staircase sequence also exhibits a mix of characteristics. At the oldest site, the upper soils tend to have anaerobic conditions and are almost pure quartz with very little P, but beneath a well-developed iron pan the soils are more nutrient rich and better drained. However, these soils beneath the pan are largely inaccessible to the plants.

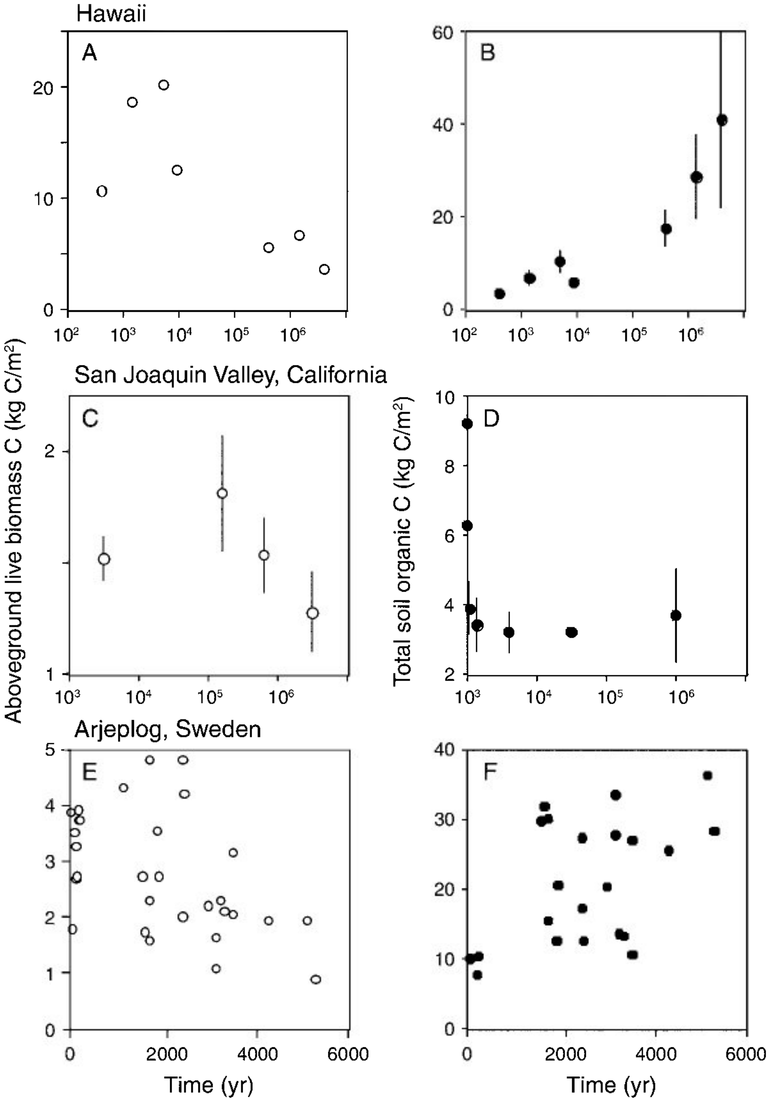

FIG. 4. Long-term changes in (A, C, E) live aboveground biomass C and (B, D, F) soil C pools for three chronosequence sites: Hawaii (Kitayama et al. 1997), California (Baisden et al. 2002), and the Swedish islands (Wardle et al. 1997, 2003). Note that the Kitayama et al. 1997 data are from a chronosequence receiving 4000 mm annual precipitation that is a parallel sequence to that presented in Table 1, which receives ~2500 mm per year. Data shown are mean soil organic C pools at each stage for each chronosequence. Soils were sampled to 22–72 cm depth in Hawaii (i.e., to parent material or iron pan layer at Hawaii), 100 cm depth in California, and through the whole soil profile to the bedrock in Sweden. Details of chronosequences are given in Table 1. Error bars show ±SD.

There are two apparent exceptions to the generality of retrogressive processes. First, it is unclear as to whether soil development in arid systems (many of which are not forested) necessarily leads to retrogression as defined by the loss of parent substrate-derived elements from the weathering zone and formation of barriers to nutrient access, or if these processes are simply slower in seasonally dry or arid areas. Examination of P status on both arid granitic and basaltic chronosequences does not support the idea of retrogression via P depletion in the same manner as observed for humid chronosequences (Lajtha and Schlesinger 1988). However, a 3-million-year sequence of the San Francisco Volcanic Field in northern Arizona includes a distinct retrogressive phase with a decline in several ecosystem processes (Selmants and Hart 2008, 2010), suggesting that retrogression is indeed possible in more arid systems over lengthy time frames. One caveat is that for very old sequences such as this, there have been major historical shifts in climate, so any classification of sites based on climatically driven variables such as precipitation needs to consider the long term history of a site, as Hotchkiss et al. (2000) have illustrated for the Hawaiian chronosequence.

Where long-term arid chronosequences do not show retrogression, three possible explanations appear relevant. First, in true arid systems, no net leaching of dissolved nutrients occurs, such that all weathering products remain in the soil column. The relevance of this mechanism can be tested by examining xeric sequences, with low rainfall concentrated during a few months of winter during which leaching occurs. In a central California xeric chronosequence, declines in productivity, shifts in mineralogy, and patterns of P cycling are observed with soil age as found elsewhere (White et al. 1996, Baisden et al. 2002). Second, mineral weathering processes may be slower in dry (and cold) conditions, as evidenced by the depletion of the primary mineral P pool over ~40 kyr (Baisden et al. 2002) in central California vs. <10 kyr in humid environments. Third, rejuvenation of rock-derived nutrient cycling may be dominated by dust inputs, rather than mineral weathering in arid environments (Fig. 2; Chadwick et al. 2003, Reynolds et al. 2006). If rock-derived elements are unavailable to plants, it is likely to be because of physical impediments to root expansion, such as the presence of highly developed pans of carbonates, sulfates, silicates and salts, all of which occlude nutrients and restrict root access in soils.

The other apparent exception to the generality of retrogession involves lowland rain forests growing in the mainland tropics. These forests often occur on old, P-poor soils that might be expected to support retrogressive forests elsewhere (Ashton 1989, Proctor et al. 1993, Sollins 1998, Kitayama 2005). Some of these forests maintain high biomass, productivity, and diversity despite experiencing significant P limitation (Ashton 1989, Proctor et al. 1993, Harrington et al. 2001), although others are shorter statured such as the campina ecosystems in Brazil or the caatinga in Venezuela (Grubb 1977, Vitousek and Sanford 1986, Tanner et al. 1998). It is difficult to directly assess the role of retrogression in inducing P limitation given that presently there is no published chronosequence of soils that includes a retrogressive phase under lowland tropical forest. One possibility is that many lowland tropical systems are sufficiently diverse that they are more likely to have species that can sustain relatively high productivity and P-use efficiency, with ever-increasing leaf N:P ratios (Reich et al. 2003, Vitousek 2004). Finally, the importance of nutrient subsidies from the atmosphere may be more important in maintaining primary productivity in tropical systems than has been previously appreciated (Okin et al. 2004, Koren et al. 2006, Boy and Wilcke 2008, Pett-Ridge 2009). These results suggest that the same principles of ecosystem development may hold in the tropics, but that retrogressive states can in many cases be represented by relatively high-biomass forests (Ashton 1989, Kitayama 2005).

Scaling up to the landscape-level

Can results from chronosequence studies of retrogression be applied to landscapes globally? Chronosequence sites are selected for their lack of variation in soil-forming factors (sensu Jenny 1941 as cited in Jenny 1980) other than age. Thus they are deliberately located on minimally eroded surfaces, so that the parent material age is approximately the same as the soil age. However, many, if not most, landscapes are dynamic, with erosion removing material at the same time as new soil is created from parent material (Porder et al. 2007). Soil age in active landscapes is more accurately described in terms of soil residence time, which is controlled by the rate of soil production at the soil-bedrock interface, the weathering zone thickness, and the rate of surface lowering. These three parameters define the timescale of soil advection, the process that brings material into the base of the weathering zone and ultimately removes it from the soil surface via erosion. In actively eroding landscapes, soil residence time is decoupled from parent material age, and it is possible to have young soils on old parent materials. This occurs where soils form on old, recently deglaciated rocks, as well as on steep slopes, and is not restricted to glaciated and mountainous regions. Even stable cratons such as those in the Amazon Basin have soil residence times that are much younger than the bedrock age. Similarly, the inputs of aerosols can significantly complicate the concept of soil residence time. For example, Okin et al. (2004) estimated that the average turnover time (inputs/pool size) for P in the upper soils in the Amazon is tens of thousands of years, while in the 4.1-million-year-old Hawaiian system, P turns over on hundred-thousand-year timescales (Vitousek 2004). Soil age and parent material age are likely different in landscapes that have been rejuvenated (e.g., glaciated), but soils and parent material are closer in age on landscapes that have not been rejuvenated for a very long time, and these latter systems are often in tropical and semi-arid areas. Hence, scaling up the results of chronosequence studies to the landscape level requires a detailed understanding of the geomorphologic and pedologic context of soil and ecosystem development.

Management of retrogressed ecosystems

Retrogressed landscapes may respond in surprising ways to management, and this is relevant in relation to the restoration or utilization of land that has properties characteristic of retrogressed systems. Based on studies of retrogressed systems in Australia, Walker et al. (2001) hypothesized that pedologically young landscapes tend to recover toward the previous state following disturbance (i.e., by having mechanisms to retain nutrients) whereas retrogressed systems can become "leaky" and may not recover critical ecosystem functions. This hypothesis highlights that disturbances should have different effects on ecosystems at different stages in their development. Further, we predict that only disturbances that rejuvenate nutrients derived from parent substrates, such as erosion or intense disturbance events, will reset ecosystems to a primary succession or progressive secondary successional stage. In contrast, disturbances that do not rejuvenate parent substrates such as fire or windthrow may increase leaching or nutrient export, and will have different effects in progressive and retrogressive ecosystems. These latter disturbances should drive retrogressive ecosystems toward a new steady state with lower biomass and complexity (Fig. 5; Suding et al. 2004). For example, Kirch (2007) applied this concept to the fate of island societies on a young, nutrient-rich island vs. an ancient, nutrient-depleted one, and concluded that the greater resilience of productive capacity on the younger island allowed the resident society to recover from overexploitation of the island's resources and to develop a more sustainable system of land management.

The mechanism underlying this hypothesis involves irreversibility of many soil processes. Ecosystems that have passed into retrogression will have a steady-state biomass that is dependent on the relative rates of nutrient inputs and outputs. Disturbance in these systems increases outputs because of their reduced capacity to retain or mobilize plant-available nutrients and ultimately maintain primary productivity and other ecosystem processes. Whether ecosystem biomass is maintained by high or by low nutrient outputs has important management implications. When inputs are high, the system is likely to recover readily from disturbance whereas when ecosystem biomass is maintained by low outputs, the capacity of the system to recover from disturbance is limited. The best documented example of the consequences of management disturbance for retrogressed systems involves the effects of land clearance on secondary tropical forest successions in northern Queensland, Australia (Winter et al. 1987, Walker and Reddell 2007). Here, following forest clearance on old, highly weathered soils, there is a decline in many ecosystem and plant community variables and the system does not follow a trajectory toward primary forest, meaning that clearance accelerates retrogression. The general implications of this are that halting an inevitable decline following disturbance may not be possible for retrogressed ecosystems.

We expect that retrogressive ecosystems could respond differently from non-retrogressed systems to future changes and drivers of global change. For example, if retrogression is caused by severe nutrient reductions, we would expect that increased subsidies of nutrients, for example through atmospheric deposition of anthropogenically derived N, may exacerbate retrogressive processes by increasing N:P ratios and thus relative P limitation. Second, globally most glaciers are actively retreating as a result of global climate change and this is set to continue for at least another 50 kyr (Houghton 2005, Raper and Braithwaite 2006). Given that increasing time since last glaciation is the factor driving retrogression in the Franz Josef and Glacier Bay chronosequences, we would expect that many more systems could potentially exhibit retrogression in the future. Third, migrations of species may affect the rate and manifestation of ecosystem retrogression, if not the end point. For example, the Franz Josef chronosequence in New Zealand is located in the "beech-gap" (i.e., a region not colonized by *Nothofagus* following the most recent glaciation). Because *Nothofagus* species are the only dominant ectomycorrhizal species in southern New Zealand, and are therefore expected to strongly influence soil nutrient availability and retention (e.g., Wardle 1991, Nezat et al. 2000, Landeweert et al. 2001, Blum et al. 2002), the return of *Nothofagus* species may have major ecosystem consequences, including increased P availability and could delay the extent or magnitude of ecosystem retrogression (Lambers et al. 2008, Dickie and Holdaway 2010). While any predictions of this type are inherently speculative, they could be resolved with careful comparative analyses or by scenario testing with ecosystem models.

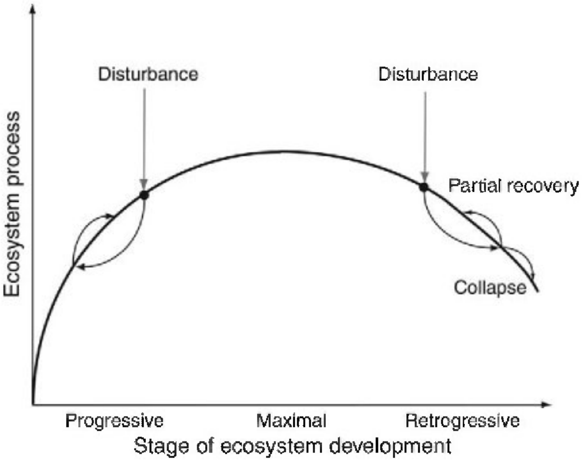

FIG. 5. Conceptual outline predicting that ecosystem responses to disturbance will vary with stage of ecosystem development. Ecosystems are predicted to be largely resilient (i.e., recovery of processes following disturbance resemble the original state) during progressive and maximal phases of ecosystem development, but to have low resilience during the retrogressive stage (modified from Walker et al. [2001]). Little is currently understood as to which ecosystem properties have thresholds or are irreversibly altered by disturbance (see Fig. 3).

SUMMARY AND RESEARCH PRIORITIES

In this review, we have explored the causes and consequences of ecosystem retrogression, at both the community and ecosystem level. Over the past few years, there has been an increasingly interdisciplinary approach applied to understanding ecosystem retrogression using chronosequence sites across the globe (Table 1). Studies on chronosequences that are of sufficient duration to include retrogressive stages have advanced our understanding of extrinsic factors in driving community and ecosystem processes in several ways. First, they serve to improve our knowledge of how long-term pedogenic changes drive shorter-term biological processes, as well as the consequences of these changes for ecosystem development. Second, they highlight that in many regions high-biomass ("climax") forests are often transient phenomena and do not persist indefinitely in the absence of rejuvenating disturbance. Third, they highlight that similar patterns of retrogression (involving reduced soil fertility, predictable shifts in organismic traits, and ecological processes) occur under vastly contrasting climatic regimes and vegetation types, even though the timescales and precise mechanisms involved may vary greatly. Fourth, they serve to advance our understanding of the linkages that occur between the aboveground and belowground subsystems over lengthy timescales, and how these change through long-term ecosystem development.

However, there are many gaps in our knowledge of retrogression that provide several unresolved, though generally tractable, questions. First, we lack knowledge of the importance of biological processes and plant-soil feedbacks relative to physical and climatic processes in controlling long-term ecosystem processes including retrogression. Second, we have limited understanding of the extent to which organic or occluded sources of N and P that are usually thought to be recalcitrant (and biologically unavailable) can support primary production during retrogression, and how patterns of belowground allocation to roots and mycorrhizal fungi change to reflect this. Third, the general importance of external nutrient subsidies for overcoming local resource limitations to ecosystem level processes is poorly understood, as is the importance of these subsidies relative to climate and parent substrate in influencing the speed and magnitude of retrogression. Fourth, most work on retrogressive chronosequences has been performed at a handful of locations, all of which have relatively low rates of soil erosion, most of which are forested and only one of which is in the humid tropics (Table 1). More work is needed to test the generality of the retrogression concept in other types of ecosystems, the extent to which erosion on steeper surfaces may delay or prevent retrogression, and whether retrogressive phenomena also occur on highly weathered P-depleted soils that characterize large areas of the tropics.

Ecosystem retrogression is of particular interest because it happens in vastly contrasting locations and leads to remarkably consistent shifts across these locations in a syndrome of ecosystem properties and processes. The common driver of retrogression across these diverse systems is the long-term reduction of the availability of P to plants. However, the speed and magnitude of retrogression varies by at least an order of magnitude across sites, and this is attributed to additional drivers such as formation of soil horizon barriers, accumulation of recalcitrant C, and atmospheric nutrient subsidies that contribute to determining how retrogression is manifested. Rapid progress in our understanding of retrogression and long-term controls of ecosystem processes can be made by evaluating these mechanisms across contrasting chronosequences. This also provides fertile ground for improving our understanding of how long-term feedbacks between biological communities and pedogenesis interact to ultimately control ecosystem development.

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